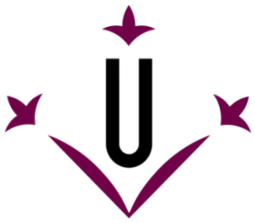

Species indicators of ecosystem recovery after reducing large herbivore density: comparing taxa and testing species combinations

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Abstract

Indicator species have been used successfully for estimating ecosystem integrity, but comparative studies for defining optimal taxonomic group remain scarce. Furthermore, species combinations may constitute more integrative tools than single species indicators, but case studies are needed to test their efficiency. We used Indicator Species Analysis, which statistically determines the association of species to one or several groups of sites, to obtain indicators of ecosystem recovery after various deer density reductions. We used five taxonomic groups: plants, carabid beetles, bees, moths and songbirds. To test whether species combinations could complement single indicator species, we used plants as a model taxon and examined the indicator value of joint occurrence of two or three plant species. Our study relies on experimental controlled browsing enclosures established for six years on Anticosti Island (Quebec). Four levels of deer density (0, 7.5 and 15 deer km^{-2} and natural densities between 27 and 56 deer km^{-2}) were studied in two vegetation cover types (uncut forests and cut-over areas), in a full factorial design for a total of eight experimental treatments. For all taxa but bees, we tested 54 treatment groups consisting in one specific density or in a sequence of two or more consecutive deer densities in one or both cover types (ten groups for bees, sampled only in cut-over areas). We found 12 plants, 11 moths and one songbird to be single species indicators of ecosystem conditions obtained under 12 different treatment groups. Six treatment groups were indicated by plants and six different ones by moths, of which one group was also identified by a songbird species. Moths were thus worth the extra sampling effort, especially since the groups they indicated were more treatment-specific (mainly one or two deer density treatments). We tested the same 54 treatment groups for plant species combinations represented by two or three co-occurring species. Plant combinations efficiently complemented plant singletons for detecting ecosystem conditions obtained under various deer densities. In fact, although singletons were highly predictive, 17 additional treatment groups were identified exclusively with two- and three-species combinations, some being more treatment-specific. Our findings show that plants and moths provide complementary indicators of ecosystem conditions

under various deer densities, and that computing species combinations increases our capacity to monitor ecosystem recovery after reducing herbivore densities.

Keywords: browsing, ecosystem management, Indicator value index (IndVal), population control, white-tailed deer

1. Introduction

Overabundant populations of large herbivores represent a threat to ecosystem integrity since they may overexploit their habitat to the point of compromising plant regeneration and the maintenance of associated fauna (Côté et al., 2004). Under certain conditions, large herbivore populations can be controlled by hunting to meet specific management goals (Conover, 2001; Lebel et al., 2012) such as reducing ungulate-human conflict (Gill, 1992) or maintaining/restoring biological diversity (Gaultier et al., 2008). To manage large herbivore populations efficiently, reliable estimates of their density are required (Morellet et al., 2007). Most estimates of herbivore density rely on direct or indirect information on the animal population itself, as for example the kilometric index (Maillard et al., 2001), pellet counts (Marques et al., 2001), harvest data or aerial counts (Pettorelli et al., 2007). Other indices focus on the browsing pressure on selected plants of the ecosystem (Anderson,1994; Koh et al., 2010). These indices are adapted to regional management of large herbivore populations and are implemented over several hundreds of km^2. However, to determine if we meet management goals, we also need to survey ecosystem recovery after implementing any management plan of large herbivore population. It is impossible to measure all ecosystem processes or the full array of species, but the identification of indicator species that could be tracked in long-term monitoring sites would be useful to determine whether ecosystem recovery is successful (Carignan and Villard, 2002). Because they focus on the impact of browsers on ecosystem integrity and have low application costs, such indicator species have high potential for monitoring and comparing sustainability of various management plans.

Indicator species have been used successfully in applied ecology for evaluating ecosystem integrity (Brooks et al., 1998; Laroche et al., 2012) or estimating ecosystem responses to disturbances like fire (Moretti et al., 2010). However, such approach has never been used to monitor ecosystem recovery after reducing large herbivore density in strongly overbrowsed ecosystems. From a management point of view, indicator species must be easy to identify and measure, sensitive to disturbances, respond to disturbances in a predictable manner, and have a narrow and constant ecological niche (Carignan and

89 Villard, 2002; Dale and Beyeler, 2001; Reza and Abdullah, 2011). Most studies adopting the indicator
90 species approach have focused on a single species or higher taxonomic group (e.g., Laroche et al.,
91 2012) even though it has been established that considering multiple taxonomic groups is likely to
92 capture the complex responses of an ecosystem to disturbances or management practices more
93 precisely (Carignan and Villard, 2002; Reza and Abdullah, 2011; Sattler et al., 2010). While multi-taxa
94 surveys may be costly, the choice of the appropriate taxonomic group or species to monitor must be
95 based on sound comparative studies, which remain surprisingly scarce in the literature (Kotze and
96 Samways, 1999; Rooney and Bayley, 2012).
97 Indicator Species Analysis (ISA) is being applied increasingly in population management (e.g.,
98 Pöyry et al., 2005; Rainio and Niemelä, 2003). Recently, methods for this type of analysis have been
99 improved in two complementary ways. First, indicator species can now be identified for groups of sites
100 (De Cáceres et al., 2010), an approach more adapted to an experimental design with multiple
101 treatments. In the context of reducing herbivore population density, this allows a given species to serve
102 as an indicator of ecosystem recovery along a range of herbivore densities. Second, De Cáceres et al.
103 (2012) recently developed a method that considers species combinations, and demonstrated that the
104 *joint* occurrences of two or more species can have a higher predictive value than data on two species
105 evaluated independently, but not strongly correlated. While these two methodological innovations have
106 substantially increased the potential of indicator species analyses, case studies that test the benefits of
107 applying them in particular contexts are still lacking. Consequently, the objectives of this study are (a)
108 to assess the complementary value of plants, insects and songbirds as potential indicator species for
109 monitoring ecosystem recovery after reducing deer densities and (b) to verify, using plants as a model
110 taxon, whether species combinations can be more efficient indicators of ecosystem recovery than single
111 species. Due to their low mobility, plants generally have site-specific requirements (soil, topography,
112 etc.) and are more subject to browsing pressure from herbivores than other guilds. For this reason, we
113 hypothesize that plant species will provide more and better indicators of ecosystem recovery than

114 insects and birds. We also hypothesize that, within insects, bees and moths will be better indicators
115 than carabid beetles since they are strongly associated with plants due to specific habitat or dietary
116 requirements. Finally, species combinations should complement the single species approach for
117 indicating particular ecosystem recovery resulting from specific reductions of deer density or from a
118 range of deer densities.

119 **2. Materials and methods**

120 *2.1. Study area*

121 Our study was carried out on Anticosti Island (7 943 km²) in the Gulf of St. Lawrence (Quebec,
122 Canada; 49° 28′N and 63° 00′W). Climate is maritime and characterized by cool summers and long but
123 relatively mild winters (for more details on climate see Beguin et al., 2009). In 1896-97, approximately
124 220 white-tailed deer were introduced on this island, which is located at *ca.* 70 km north of the
125 north-eastern limit of the species' distribution range. Theoretical model suggests that the deer
126 population has increased rapidly, reaching a peak about 30 years after its establishment and then
127 gradually stabilized at its current level (Potvin et al., 2003), which is estimated at >20 deer km^{-2}.
128 Population fluctuations are mostly related to winter severity (Potvin and Breton, 2005) as the island is
129 presently void of predator. The indigenous black bear (*Ursus americanus*) was abundant on the island
130 at the introduction time, but rapidly became rare (1950s) and then extinct (1998) likely due to the
131 disappearance of wild berries due to deer overbrowsing (Côté, 2005). Ecological conditions of
132 Anticosti Island have not been as favourable for other introduced large herbivores that have
133 disappeared (bison, wapiti, caribou) or remained at low density, like moose (*Alces alces;* 0.04 moose
134 km^{-2}; Beaupré et al., 2004).

135 The forests of Anticosti belong to the boreal zone. They are naturally dominated by *Abies*
136 *balsamea*, *Picea glauca* and *P. mariana*, while deciduous tree species (*Betula papyrifera*, *Populus*
137 *tremuloides*, *P. balsamifera*) occur sporadically. Despite the short history of deer herbivory on the
138 island, the impacts of deer browsing on the structure, composition and dynamics of forest ecosystems

139 have been extensive (Potvin et al., 2003; Tremblay et al., 2006). For instance, the surface covered by *A.*
140 *balsamea* stands, a key habitat for winter survival of deer, has been reduced by half over the last
141 century and replaced by *P. glauca* stands (Potvin et al., 2003; Tremblay et al., 2007). Furthermore, the
142 shrub layer has been almost entirely eliminated and the most palatable ubiquitous woody plant species
143 such as *Acer spicatum*, *Cornus sericea* subsp. *sericea*, *Corylus cornuta*, and *Taxus canadensis*, have
144 almost been extirpated (Pimlott, 1963; Potvin et al., 2003). A recent study also showed that the
145 community composition of bees and moths, two groups of insects strongly associated with vegetation,
146 has been modified by deer overabundance, while the abundance and community composition of carabid
147 beetles, most of which have no direct trophic relations with plants, do not vary with deer density
148 (Brousseau et al., 2013). Deer over-browsing on the island has also changed the community
149 composition of songbirds and reduced the occurrence of species dependent on the understory (Cardinal
150 et al., 2012a, 2012b).

151 *2.2. Experimental Design*

152 Our study benefited from the infrastructure of a long-term experiment that was initiated in 2001 and
153 designed to investigate the impact of reducing deer density on the reproduction and growth of plants in
154 two vegetation cover types: uncut forests and cut-over areas. This experimental set-up is a full factorial
155 split-plot design with main plots replicated in three complete randomized blocks (located between
156 4 and 71 km apart). Each block was composed of four main plots (adjacent or in close proximity within
157 each block). They consisted of three large enclosures with distinct deer densities (0, 7.5, 15 deer · km^{-2})
158 and a control situation outside the fence (*in situ* densities: 27, 56 and 56 deer · km^{-2}). To control deer
159 density, all deer were removed from all enclosures each year. No deer were reintroduced in a 10-ha
160 enclosure (0 deer · km^{-2}), whereas three deer were stocked yearly in each of the two other enclosures,
161 one measuring 40 ha (7.5 deer · km^{-2}) and the other 20 ha (15 deer · km^{-2}). Deer (yearlings or adults)
162 were captured in early spring, released within enclosures and culled in late autumn. Deer enclosures
163 were closely monitored to detect and subsequently repair any broken fences, and thereby impede

intruders as well as deer escape, injury or fatality. Deer stocking began in 2002 and was repeated annually until 2009. The *in situ* deer densities were monitored on unfenced sites using distance sampling of summer pellet groups on permanent transects cleared of feces each spring (Tremblay et al., 2006). The subplots of uncut forest and cut-over areas were staked in all blocks simultaneously, in the summer of 2001. Both types of vegetation cover were characterized by >70% balsam fir canopy cover before the beginning of the experiment. The cut with protection of soil and regeneration method was used, and all trees >9 cm at breast height were removed over about 70% of the area, leaving about 30% of the mature balsam fir forest in isolated patches (mean size of uncut forest patches was 5.9 ± 8.2 ha). Cut-over was included in the design because it has been used on Anticosti as a catalyst to stimulate balsam fir regeneration since 1995 (Beaupré et al., 2005).

2.3. Sampling procedures

Five taxonomic groups belonging to different guilds, with distinct habitat requirements and mobility, were selected as model groups: 1) plants, which are sessile producers influenced by local edaphic conditions, 2) carabid beetles, which are mostly epigeic predators with low dispersal ability and weak association with vegetation, 3) bees (Apoidea, excluding former Sphecoidea), which are nectar- and polliniphagous, thus strongly associated with plants, and have high dispersal ability, 4) moths (superfamilies Bombycoidea, Drepanoidea, Geometroidea, Noctuoidea which represent the great majority of macro Lepidoptera), most of which are phytophagous with larvae being mostly sessile and generally feeding specifically on their host plants, while adults have varying dispersal ability and are mainly nocturnal, and 5) songbirds which have high dispersal ability, feed and nest on different vegetation layers or on the ground, and thus are strongly associated with stand structure. All taxa were surveyed six years after establishment of the experiment. All scientific names followed the Integrated Taxonomic Information System (ITIS, 2012) except for moths for which we used the taxonomy of Moth Photographers Groups of Mississippi State University (2013).

Plants were sampled in 20 permanent quadrats (10 × 10 m) randomly positioned in 2001 in both

189 vegetation cover types (uncut forests and cut-over areas) in each of the 12 main plots (n = 480
190 quadrats). Data from three quadrats of the *in situ* density in uncut forests were not used, due to a large
191 windfall that disturbed them (n = 477). The remaining quadrats were subdivided into 100 subquadrats
192 of 1 × 1 m, two of which were selected randomly for surveys. In each subquadrat, the horizontal cover
193 of each vascular plant species was estimated according to 12 percent cover classes (<1, 1–5, 10 classes
194 up to 95, 95–100%). Cover of trees and shrubs smaller than 2.5 m was included in the survey, while
195 taller individuals were not surveyed because they were inaccessible to deer and because they were
196 unadapted to the sub-quadrat size.

197 Carabid beetles were sampled by Brousseau et al. (2013) using Luminoc® traps (Jobin and
198 Coulombe, 1992) as pitfall traps to attract a large diversity and abundance of beetles (Hébert et al.,
199 2000). In each of the 12 main plots, two pitfall traps were installed in each vegetation cover type (uncut
200 forests and cut-over areas) and an internal recipient was filled with 40% ethyl alcohol as a preservative
201 (n = 48 traps). Traps were placed at least 100 m away from fences, and, whenever possible (i.e., when a
202 forest patch was large enough), at least 50 m from forest edges. The distance between traps was at least
203 50 m, far enough to ensure that traps were independent from each other. Traps were operated for five
204 periods of 9-11 days between June 15 and August 15, 2007 (i.e., the main activity period for ground
205 dwelling insects in the region). At the end of each pitfall-trapping period, internal recipients were
206 removed and samples transferred into collecting jars. Then, traps were raised and placed on a post at
207 three meters above the ground to sample flying adult Lepidoptera for five periods of 3-4 days. Traps
208 were set to collect adult Lepidoptera when three consecutive non-rainy days were forecast. Moths were
209 killed by Vapona® strips placed in the traps; no preservative was used. Adult bees were sampled using
210 one Malaise trap (Gressit and Gressit, 1962) per main plot. Traps were installed only in cut-over areas
211 (n = 12 traps), where bees were expected to be mostly active; they usually avoid closed forests. Traps
212 were located 100 m from fences and at least 50 m from forest edges and were in constant operation
213 from June 15 to August 15, 2007. We defined the abundance of the different insect taxa as the number

214 of individuals trapped within their sampling periods. A reference collection of the three insect groups is
215 available at the Laurentian Forestry Centre in Quebec City.
216 The relative abundance of songbirds was surveyed by Cardinal (2012b) in 2007 using point
217 counting during the nesting period (Bibby et al., 2000). In each main plot, two point-counts with a 30 m
218 radius were centered on randomly selected uncut forests, and three point-counts separated by at least
219 100 m were located randomly in cut-over areas (n = 60 point-counts). More point-counts were located
220 in cut-over areas since they represented 70% of each main plot on the experimental site, whereas uncut
221 forests represented 30%. A 50 m buffer zone was maintained along fence or forest edges to avoid edge
222 effects. Individual songbirds were counted for each species heard over a period of 20 minutes. Each
223 point-count was visited six times from June 5 to 30, between 4:30 and 10:00 am, always under
224 favorable weather conditions, i.e., without rain or strong winds. We defined the abundance of songbird
225 species at each point-count as the highest count of individuals of a given species among all visits at that
226 station during the sampling season, a reliable proxy for true abundance (Toms et al., 2006).
227 *2.4. Statistical analysis*
228 Five independent Indicator Species Analyses (ISA) were carried out to identify individual plant,
229 carabid beetle, bee, moth, and songbird indicators of ecosystem recovery after reducing deer
230 populations at various densities. For this purpose, five species matrices were assembled using the
231 abundance data of the different taxa, i.e., percentage cover for plants and number of individuals for
232 insects and songbirds. Rare species were removed from the database. For plants, this corresponds to the
233 species surveyed in less than 5% of the quadrats (n = 93). Rare insect species were those captured less
234 than four times (n = 55) and rare bird species (n = 7) were those surveyed in only one point-count. A
235 total of 167 species were then used in subsequent analyses (see Supplemental Material – Appendix A).
236 Logarithmic transformation was performed on all matrices to reduce the influence of extreme
237 abundance values (Legendre & Legendre, 1998). ISA was carried out on each matrix to identify
238 individual species strongly associated with specific treatment groups, using the function ‘multipatt’ of

239 the ‘indicspecies’ package in R (De Cáceres and Legendre, 2009; De Cáceres et al., 2010). For plants,
240 carabid beetles, moths, and songbirds, eight treatments were tested (i.e., four classes of deer density *
241 two vegetation cover types), which would result in 255 (= $2^8 - 1$) possible treatment groups. However,
242 we restricted our analyses to the 54 treatment groups that could be interpreted ecologically. These
243 consisted in a particular deer density or in a sequence of two or more consecutive deer densities in one
244 or both cover types (Fig. 1). In other words, we excluded treatment sequences consisting of non-
245 consecutive densities like 0 and 15 deer km^{-2}, as they would not be interpretable ecologically. In the
246 case of bees, only four treatments were tested, i.e. four levels of deer density in the cut-over areas.
247 Among the 15 (= $2^4 - 1$) possible treatment groups, ten were deemed to be meaningful ecologically,
248 while the others were excluded from the analysis. As association function, we used the Indicator Value
249 (IndVal) index corrected for unequal group sizes (De Cáceres and Legendre, 2009; Dufrêne and
250 Legendre, 1997). This index is a product of the degree of specificity (A; uniqueness to a particular
251 group) and the degree of fidelity (B; frequency of occurrence within a particular group) of species in
252 groups defined *a priori*. We discarded species with a low indicator value by setting a threshold for
253 components A and B (A = 0.6 and B = 0.25; thresholds suggested by De Cáceres et al., 2012). To
254 assess the significance of each species, we performed a restricted permutation test (n = 999) where the
255 quadrats within each block could be exchanged, but quadrat exchange from one block to another was
256 not permitted. This manipulation controlled for the block effect and allowed us to identify indicator
257 species only linked to deer density treatments and vegetation cover type.
258 We used plants as a model taxon to evaluate the efficiency of species combinations for indicating
259 ecosystem recovery under various treatment groups of deer density reductions. For this additional
260 analysis, we assembled a new matrix with double combinations (two co-occurring species), and triple
261 combinations (three co-occurring species) using the function ‘combinespecies’ of the ‘indicspecies’
262 package (De Cáceres et al., 2012). A new ISA was then performed according to the method described
263 above. To compare the number of indicators found in single species (singletons) with those found in

two- and three species combinations, we corrected *p*-values with Hochberg's method (1988). Since many combinations were significant, we discarded indicators with a low predictive value by setting the same threshold values for ISA components as above (A = 0.6 and B = 0.25; De Cáceres et al., 2012). Then, as suggested in De Cáceres et al. (2012), we eliminated indicators with an occurrence group completely nested within the occurrence group of others since they added no information. We then selected a subset of indicators that would maximize coverage values, i.e. the number of permanent quadrats in which at least one of the final indicators was present. This subset was fixed at a maximum of four indicators (single species as well as two- or three species combinations).

3. Results and Discussion

3.1. Single indicator species

Among the 167 common species recorded, 22 species (12 plants, 11 moths and 1 songbird) were found to be indicators of 12 different groups resulting from deer density treatments (Fig. 2). Each taxa indicated different groups: six groups were indicated by plants and six others by moths, of which one group was also indicated by one songbird species. No indicator species of deer density treatments were found among bees and carabid beetles. For the latter, many of the species found were predators (both larvae and adults) of arthropods, and thus perhaps less sensitive to changes in plant communities induced by deer browsing (Brousseau et al., 2013). As well, highly mobile organisms, such as bees and birds can more easily find food and nesting sites outside treated areas. For such organisms, habitat selection is also determined by large-scale attributes (Bélisle et al., 2001; Diaz-Forero et al., 2013) and thus, might be less dependent of conditions generated by deer density reductions, which could explain their lack of association with particular treatments.

Plants generated indicator species for treatment groups mainly in cut-over areas (4 of 6 groups), whereas moths and songbirds identified treatment groups only in uncut forests (all 6 groups; Fig. 2). Groups revealed by fauna were more treatment-specific (three groups corresponding to one or two deer density treatments) than those shown by plants. For plants, in uncut forests, *Taraxacum officinale* was

289 found to be an indicator of sites with reduced deer density (7,5 and 15 deer km^{-2}; group # 47; Fig. 2A).
290 For cut-over areas, *Chamerion angustifolium* was clearly associated with low deer density (0 and 7.5
291 deer km^{-2}; # 11, 48). This plant species has been previously identified as preferred forage for deer and
292 moose (Daigle et al., 2004; Dostaler et al., 2011) and one that also recovers quickly when deer densities
293 are controlled (Tremblay et al., 2006). The species *Mitella nuda* and *Viola macloskeyi* were associated
294 with the presence of deer in cut-over areas, independently of density (# 54). Three species typical of
295 boreal forests, *Cornus canadensis*, *Linnaea borealis* and *Maianthemum canadense*, indicated reduced
296 deer densities (between 0 and 15 deer km^{-2}) in cut-over areas (# 52).
297 For insects, we found two general groups in our study, whether species were associated with high
298 or low deer density treatments. Within these general, we distinguished more specific responses. We
299 found three moth species associated with the presence of deer in uncut forests: two were associated
300 with the presence of deer, regardless of its density (# 25), while another one (*Macaria marmorata*) was
301 indicator of high deer densities (#17, 15 deer km^{-2} and *in situ*). Thus, these species have been favoured
302 by the introduction of white-tailed deer on Anticosti Island. On the other hand, several species showed
303 an opposite response and have thus been negatively impacted by deer introduction on the island. For
304 instance, five moth species were individually indicative of reduced deer density, but with a correlation
305 insufficient for discriminating between a slight or strong reduction or even complete absence of deer (#
306 24). All these species feed on herbaceous plants (e.g., *Taraxacum, Polygonum, Fragaria*), ericaceous
307 plants (e.g., *Kalmia, Vaccinium*) or deciduous shrubs (e.g., *Rubus, Betula, Prunus*) (Handfield, 2011).
308 These plants react rapidly to reduced deer density (Tremblay et al., 2006) and associated moths are thus
309 useful indicators of ecosystem recovery, but not of specific conditions. Other species were associated
310 with more specific conditions. Indeed, *Cabera variolaria*, was associated with uncut forest where deer
311 density was reduced at 15 deer km^{-2} (# 4) while *Syngrapha viridisigma* was associated with the absence
312 of deer in uncut forests (#2; Fig. 2B). Larvae of this last species feed mainly on *Abies balsamea* and
313 *Picea glauca* (Handfield, 2011), species that are present in all sites, thus suggesting that adults may

benefit from the presence of flowering plants in cut-over areas. A special group was indicated by *Palthis angulalis* which was associated with all conditions except cut-over areas in stands with *in situ* deer density. Larvae of this species feed preferentially on balsam fir (Handfield, 2011) but they are known to be polyphagous (Wagner, 2005). Our results suggest that, under *in situ* deer density, this species has maintained its population on balsam fir in uncut forest but it may also benefit from the presence of flowering plants in cut-over areas or might be opportunistic in exploiting newly available host plants in all habitats when deer density is reduced. As for the white-tailed deer, the combination of a balsam fir forest cover close to cut-over areas with abundant and diverse plant resources may also be a good habitat combination for several insects.

Previous studies have shown both a shift in moth abundance and diversity under high herbivore pressure (Brousseau et al., 2013; Brown, 1997; Kruess and Tscharntke, 2002; Pöyry et al., 2005) but this is the first time we identify species indicators of ecosystem recovery after reducing herbivore density. The interpretation of habitat specificity of moth catches in light traps is challenging and we made it with caution because it integrates ecological needs of larvae, that are quite well known, and of adults which are poorly known. In fact, at larval stages, moths (Lepidoptera) feed on specific host plants, but when they become adults, they are mobile and can distribute widely to find food, mates or egg-laying sites (Ehrlich and Raven, 1964; Ricketts et al., 2002). Moreover, habitat specificity inference might be affected by light attraction. Nevertheless, Kitching et al. (2000) successfully used large Pennsylvania light traps for identifying moth indicators of ecosystem fragmentation in Australia. The Luminoc™ traps used in our study are small portable light traps (light tube of 1,8 W) that obviously have smaller radius of attraction than the Pennsylvania light trap, and thus represents a powerful tool for identifying moth indicator species in ecological restoration programs.

Finally, one songbird (*Loxia leucoptera*) was indicator of high deer densities in uncut forests (#17, 15 deer km^{-2} and *in situ*). This songbird species is associated to higher canopy of conifer forests and is therefore probably unrelated to ecosystem change due to deer density (Benkman, 1987; 1993). As this

339 was the only songbird species found indicator, bird survey would be redundant with a moth survey in
340 this context.
341 *3.2. Indicator species combinations (plants)*
342 Our analyses of plant data on single species as well as on two- and three-species combinations
343 allowed us to find valid indicators for 23 deer density groups out of the 54 tested (see Supplementary
344 Material – Appendix B for the complete list of indicators). Indicators were found for two additional
345 groups, but they discriminated between uncut forests and cut-over areas rather than between deer
346 densities and were therefore not considered here. It is striking that only five treatment groups were
347 identified by singletons alone, and one was revealed by a singleton and a three-species combination,
348 whereas 17 additional treatment groups were revealed exclusively by two- or three-species
349 combinations (Fig. 3). For each group, the number of valid indicators was highly variable, ranging
350 from 1 to 97 (Table 1). However, many of these were spatially redundant and high coverage values
351 were generally obtained with less than four indicators. The coverage of the final set of indicators (i.e.,
352 the percentage of permanent vegetation quadrats where the indicators were found for a particular
353 group) ranged from 29 to 99% (Table 1). The three treatment groups with the highest coverage (# 11,
354 51 and 52) were among those indicated by singletons alone. For example, for group #11, corresponding
355 to low deer density in cut-over areas (0 and 7.5 deer km^{-2}; Fig. 1), there were 97 valid indicators,
356 among which one singleton alone, *Chamerion angustifolium*, was sufficient to reach a coverage of 83%
357 (Table 1). In other words, this species was present in 83% of the permanent vegetation quadrats
358 sampled in cut-over areas of 0 and 7.5 deer km^{-2}. The other indicators did not contribute to increasing
359 the coverage for this group further, since they were localized in a subset of the same quadrats.
360 Among the 18 treatment groups with valid two- or three-species combination indicators, the final
361 indicators of only 11 groups had a coverage $\geq$ 50% and were thus frequent enough to be useful
362 indicators of ecosystem conditions under various deer density (Table 1; Fig. 3). We used treatment
363 group #13 to illustrate how to interpret the results of the species combination indicator analyses. The

364 presence of *Oxalis montana* along with *Trientalis borealis* in uncut forests or that of *Abies balsamea*
365 with *Dryopteris carthusiana* and *Trientalis borealis* (Supplementary Material – Appendix B) would
366 indicate ecosystem recovery to a large extent as these forest conditions were obtained by reducing deer
367 density at ≤ 7.5 deer km^{-2} (group #13). One or both combinations should be found in about 68% of this
368 deer density-vegetation group. Finally, species combinations allowed indicating more specific
369 treatment groups than singletons and a much larger number of groups, thus maximising data usefulness
370 (Figs. 1 and 3).

371 **4. Conclusions**

372 Our findings illustrate how moth surveys can complement plant surveys for monitoring ecosystem
373 recovery after reducing deer densities, since each of these taxa revealed different groups of deer
374 reduction treatment. Plants were particularly useful in cut-over areas, and moths only in uncut forests.
375 The extra sampling for moth surveys could thus be focused most productively in forests during future
376 assessments. Sampling moths was particularly valuable, since they were closely associated with more
377 specific groups generated by various deer densities than plants. Among plants, calculating two- and
378 three species combinations clearly increased the array of deer density groups for which significant
379 indicators were found. Although single plant species (singletons) were highly predictive and showed
380 extensive coverage, they were able to detect only six deer density groups, whereas 17 additional
381 groups, several being more specific, were identified with two- and three-species combinations. Species
382 combinations thus seem to complement singletons for improving our capacity to detect more specific
383 ecosystem conditions generated by various deer densities.

384 By focusing on a subset of species, Indicator species analysis (ISA) can be an effective tool for
385 wildlife managers because it simplifies the assessment of ecosystem conditions resulting from
386 management plans aimed to reduce large herbivore density. ISA is considerably improved by
387 combining groups of sites (i.e., deer density treatments in our case) as well as by considering species
388 co-occurrences as indicators. While treatment grouping can be useful to overcome the arbitrary

389 delimitation of treatments in experimental design, species combinations may be useful for identifying
390 indicator of a higher number of treatment groups.
391 Although we developed our approach with species abundance data, it could be used with
392 presence/absence data, which may significantly reduce the inter-observers error compared to other
393 approaches based on counts. Our study is based on data collected six years after we began reducing
394 deer densities. Therefore, our indicators are species that responded rapidly to deer density treatments.
395 Several of these species are useful indicators of a rapid ecosystem recovery. In further studies, it would
396 be important to include time series to identify indicators along succession, especially under logging
397 treatment as plant succession change quickly after cutting. Even though our results relate to the precise
398 case of boreal forests, the approach remains applicable to deciduous forests where deer populations
399 thrive and even to other herbivore systems worldwide, as long as a new Indicator Species Analysis is
400 conducted with local species pool. Finally, other issues remain to be explored, for example, how to
401 better exploit the indicator value of combinations of taxa belonging to different taxonomic groups (e.g.
402 plants and insects), an approach that could be called "community indicator analysis".

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Table 1

Results of the indicator species analysis for plants, for each of the 54 deer density groups (see Fig. 1 for group descriptions). Sites: Number of permanent quadrats (10 × 10 m) belonging to each deer density group; Valid: Number of valid indicators detected (p-value < 0.05; A ≥ 0.6 and B ≥ 0.25); Final: Smallest set of valid indicators (maximum of four); Coverage: Percentage coverage of the final set of valid indicators; i.e., the percentage of permanent quadrats in which at least one of the final indicators was present.

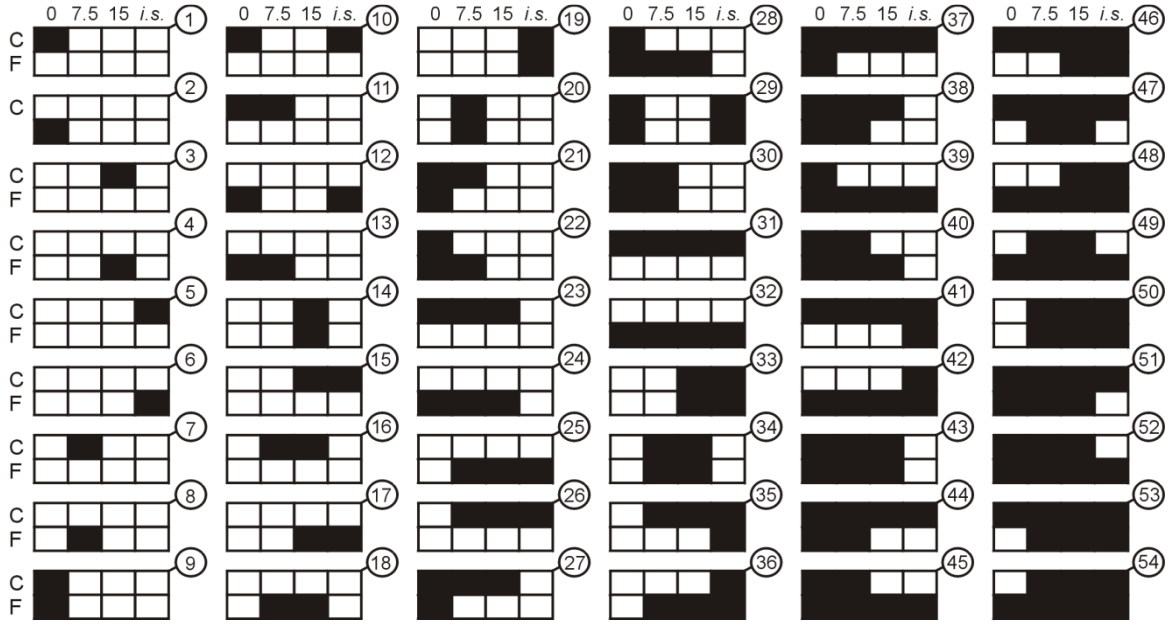
N. group	Sites	Valid	Final	Coverage	N. group	Sites	Valid	Final	Coverage
1	60	0	0	0	28	240	0	0	0
2	60	0	0	0	29	237	0	0	0
3	60	0	0	0	30	240	0	0	0
4	60	0	0	0	31	240	70	4	87
5	60	4	2	33	32	237	40	4	77
6	57	0	0	0	33	237	0	0	0
7	60	4	4	50	34	240	0	0	0
8	60	0	0	0	35	237	0	0	0
9	60	0	0	0	36	237	0	0	0
10	120	0	0	0	37	300	6	2	52
11	120	97	1	83	38	300	2	2	36
12	117	0	0	0	39	297	3	1	39
13	120	5	2	68	40	300	0	0	0
14	120	0	0	0	41	297	9	4	54
15	120	0	0	0	42	297	7	4	56
16	120	2	2	46	43	360	7	4	60
17	117	0	0	0	44	360	4	2	52
18	120	0	0	0	45	357	0	0	0
19	117	0	0	0	46	357	3	3	56
20	120	0	0	0	47	360	2	2	44
21	180	0	0	0	48	357	35	1	63
22	180	0	0	0	49	357	3	2	45
23	180	36	4	78	50	357	0	0	0
24	180	1	1	29	51	420	60	4	95
25	177	0	0	0	52	417	88	3	99
26	180	0	0	0	53	417	5	3	52
27	240	9	3	45	54	417	24	2	69

Figure captions

Figure 1. The 54 deer density groups (group number circled) tested to identify indicator species of deer density (0, 7.5, 15 deer km^{-2}, *i.s.* = in situ deer density between 27 and 56 deer km^{-2}) and two vegetation cover types (C = cut-over areas; F = uncut forests). Deer density groups refer to a particular deer density or to a sequence of two or more deer densities that are consecutive in one or both cover types (black squares). The figure is a schematic representation of the treatments (deer density and vegetation cover types) in the experimental design and not the spatial arrangements of the plots. For plants, ground beetles, moths and songbirds, the tested groups were selected among 255 possible groups, after eliminating those without ecological significance (see methods). Since only cut-over areas were sampled for bees, the 10 following groups were tested among the 15 possible ones: 1, 3, 5, 7, 10, 11, 15, 16, 23, and 26.

Figure 2. Single species indicators of deer density groups among plants, moths, and songbirds (group number circled, see Fig. 1). The specificity (A), sensitivity (B) and indicator value (IV) are presented. C = cut-over areas; F = uncut forests; *i.s.* = *in situ* deer density between 27 and 56 deer km^{-2}.

Figure 3. Coverage of single plant species indicators as well as two- and three plant species combinations for the 23 deer density groups. Coverage represents the percentage of permanent quadrats (10 x 10 m) in which at least one of the final indicators of a particular group is present. Valid indicators are those significant at *p-value* ≤ 0.05, with a specificity (A) value ≥ 0.6 and a sensitivity (B) ≥ 0.25. Refer to Table 1 for the number of valid indicators of each group and to Fig. 1 for the description of deer density groups.


0 7.5 15 i.s.
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584 **Fig.2**

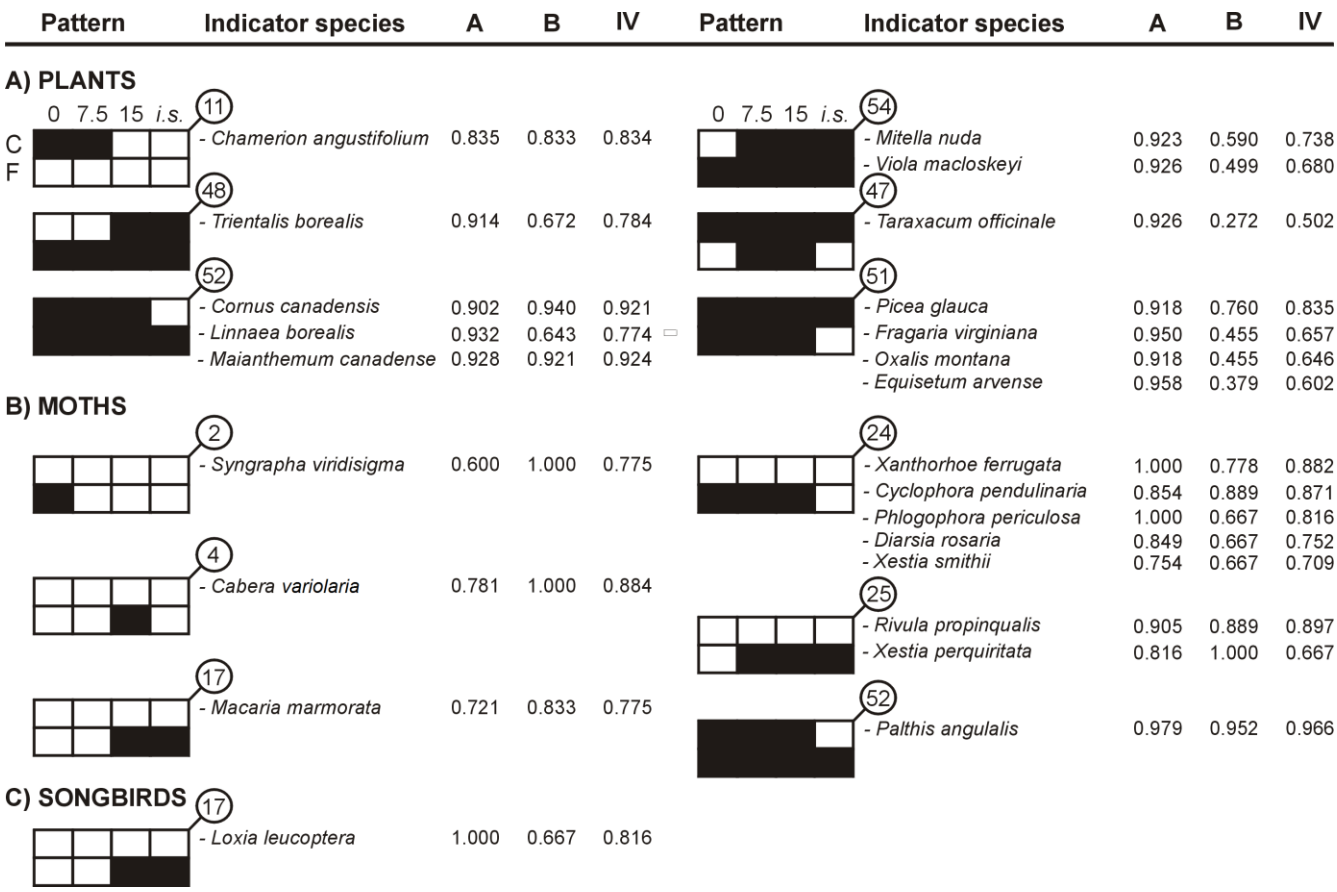
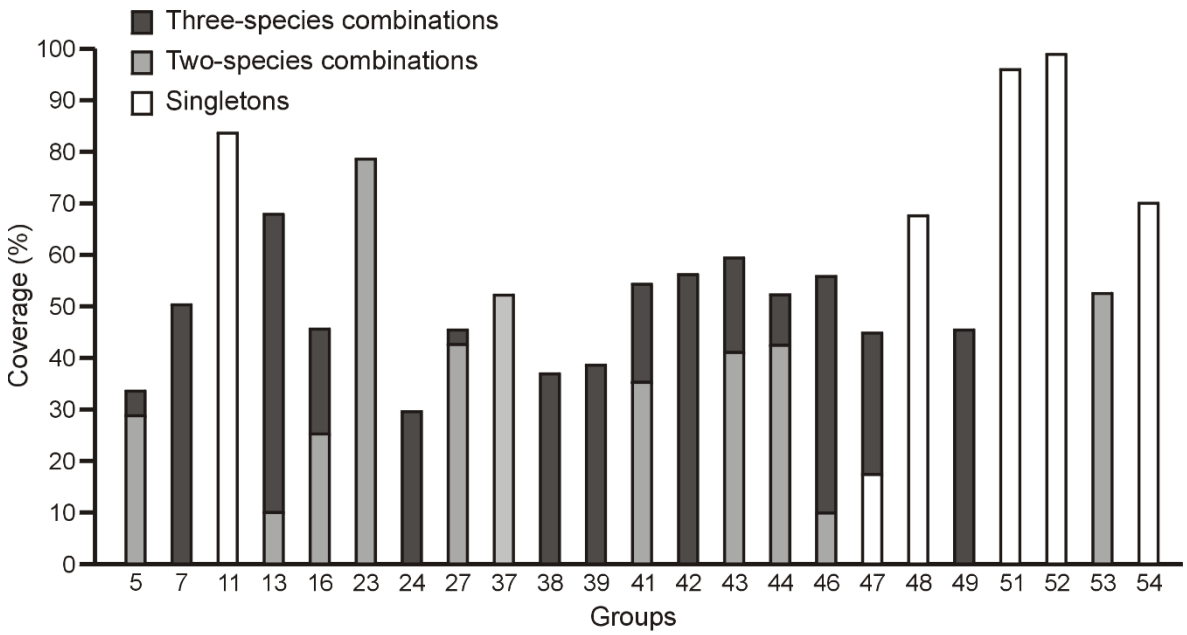

Pattern
Indicator species
A
B
IV
Pattern
Indicator species
A
B
IV
A) PLANTS
0 7.5 15 i.s.
C
F
11
- Chamerion angustifolium 0.835 0.833 0.834
48
- Trientalis borealis 0.914 0.672 0.784
52
- Cornus canadensis 0.902 0.940 0.921
- Linnaea borealis 0.932 0.643 0.774
- Maianthemum canadense 0.928 0.921 0.924
B) MOTHS
2
- Syngrapha viridisigma 0.600 1.000 0.775
4
- Cabera variolaria 0.781 1.000 0.884
17
- Macaria marmorata 0.721 0.833 0.775
C) SONGBIRDS
17
- Loxia leucoptera 1.000 0.667 0.816
0 7.5 15 i.s.
54
- Mitella nuda 0.923 0.590 0.738
- Viola macloskeyi 0.926 0.499 0.680
47
- Taraxacum officinale 0.926 0.272 0.502
51
- Picea glauca 0.918 0.760 0.835
- Fragaria virginiana 0.950 0.455 0.657
- Oxalis montana 0.918 0.455 0.646
- Equisetum arvense 0.958 0.379 0.602
24
- Xanthorhoe ferrugata 1.000 0.778 0.882
- Cyclophora pendulinaria 0.854 0.889 0.871
- Phlogophora periculosa 1.000 0.667 0.816
- Diarsia rosaria 0.849 0.667 0.752
- Xestia smithii 0.754 0.667 0.709
25
- Rivula propinqualis 0.905 0.889 0.897
- Xestia perquiritata 0.816 1.000 0.667
52
- Palthis angulalis 0.979 0.952 0.966

Fig.2



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589 **Fig. 3**

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Supplementary Material

Appendix A. List of species sampled in the controlled browsing experiment on Anticosti Island and used in the analysis

PLANTS			
Abies balsamea	*Coptis trifolia*	*Lycopodium annotinum*	*Ranunculus acris*
Athyrium filix-femina	*Cornus canadensis*	*Lycopodium clavatum*	*Ribes lacustre*
Betula papyrifera	*Dryopteris carthusiana*	*Maianthemum canadense*	*Rubus idaeus*
Bromus ciliatus	*Elymus repens*	*Mitella nuda*	*Rubus pubescens*
Calamagrostis canadensis	*Equisetum arvense*	*Nabalus trifoliolatus*	*Schizachne purpurascens*
Carex capillaris	*Equisetum scirpoides*	*Oryzopsis asperifolia*	*Solidago macrophylla*
Carex laxiflora	*Equisetum. sylvaticum*	*Osmorhiza claytonii*	*Streptopus lanceolatus* var. *lanceolatus*
Cerastium fontanum	*Fragaria virginiana*	*Oxalis montana*	*Taraxacum officinale*
Chamerion angustifolium	*Galium trioflorum*	*Packera aurea*	*Trientalis borealis*
Cirsium arvense	*Gaultheria hispidula*	*Petasites frigidus* var. *palmatus*	*Vaccinium myrtilloides*
Cirsium vulgare	*Gymnocarpium dryopteris*	*Picea glauca*	*Vaccinium vitis-idaea*
Clintonia borealis	*Linnaea borealis*	*Picea mariana*	*Viola macloskeyi*
Conioselinum chinense	*Listera cordata*	*Poa palustris*	
MOTHS			
Amphipoea americana	*Ecliptopera silaceata albolineata*	*Idia americalis*	*Speranza bitactata*
Anaplectoides pressus	*Eilema bicolor*	*Lacanobia radix*	*Syngrapha viridisigma*
Cabera erythemaria	*Enargia infumata*	*Leucania multilinea*	*Xanthorhoe abrasaria congregata*
Cabera variolaria	*Epirrhoe alternate*	*Protodeltote albidula*	*Xanthorhoe ferrugata*
Caripeta divisata	*Eulithis explanata*	*Macaria marmorata*	*Xanthorhoe iduata*
Cyclophora pendulinaria	*Eupathica spp.*	*Mesoleuca ruficillata*	*Xanthorhoe decoloraria*
Dasychira plagiata	*Euphyia intermediate*	*Palthis angulalis*	*Xanthotype urticaria*
Diarsia dislocate	*Euplexia benesimilis*	*Phlogophora periculosa*	*Xestia homogena*
Diarsia jucunda	*Euxoa dissona*	*Rheumaptera hastata gothicata*	*Xestia mixta*
Diarsia rosaria	*Habrosyne scripta*	*Rivula propinqualis*	*Xestia perquiritata*
Diarsia rubifera	*Horisme intestinata*	*Scopula frigidaria*	*Xestia smithii*
Dysstroma citrata	*Hydriomena divisaria frigidata*	*Scopula junctaria*	
Dysstroma truncate transversata	*Hyppa xylinoides*	*Spargania magnoliata*	

593 **Appendix A.** Continued

BEES			
Andrena spp.	*Bombus ternarius*	*Lasioglossum foxii*	*Megachile relativa*
Anthophora terminalis	*Coelioxys germana*	*Lasioglossum quebecence*	*Megachile frigida*
Bombus borealis	*Colletes consors*	*Lasioglossum rufitarse*	*Osmia proxima*
Bombus fernaldae	*Colletes impunctatus*	*Lasioglossum (Dialictus) spp.*	*Osmia tersula*
Bombus frigidus	*Halictus confuses*	*Megachile inermis*	
Bombus insularis	*Halictus rubicundus*	*Megachile melanophaea*	
GROUND BEETLES			
Amara aulica	*Harpalus rufipes*	*Pterostichus melanarius*	*Synuchus impunctatus*
Calathus advena	*Harpalus somnulentus*	*Pterostichus pensylvanicus*	
Calathus ingratus	*Pterostichus adstrictus*	*Pterostichus punctatissimus*	
Harpalus fulvilabris	*Pterostichus coracinus*	*Sphaeroderus nitidicollis nitidicollis*	
SONGBIRDS			
Catharus guttatus	*Dendroica striata*	*Melospiza lincolnii*	*Tachicineta bicolore*
Catharus ustulatus	*Dendroica tigrina*	*Passerella iliaca*	*Troglodytes troglodytes*
Certhia americana	*Dendroica virens*	*Picoides villosus*	*Turdus migratorius*
Colaptes auratus	*Empidonax alnorum*	*Poecile hudsonicus*	*Vermivora peregrina*
Contopus cooperi	*Empidonax flaviventris*	*Regulus calendula*	*Vireo philadelphicus*
Dendroica castanea	*Geothlypis trichas*	*Regulus satrapa*	*Wilsonia pusilla*
Dendroica coronata	*Junco hyemalis*	*Sitta Canadensis*	*Zonotrichia albicollis*
Dendroica magnolia	*Loxia leucoptera*	*Spinus pinus*	

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